The Science of Social Vision
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Faces, Bodies, Social Vision as Agent Vision, and Social Consciousness

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Abstract and Keywords

This chapter discusses recent findings from research on face and body perception giving special attention to the implications of the findings for social vision. The first section is devoted to similarities between the processes underlying face and body perception. The second section discusses how the perception of faces and bodies is integrated. The third section tackles issues on conscious and nonconscious perception of socially meaningful signals and their neuroanatomical underpinnings. Finally, the relation between social vision and awareness is explored, and notion of social consciousness is developed. Throughout the chapter, the notions of agent vision and social vision are used in the sense made familiar by the expression “night vision” to refer to various devices that expand the normal visual abilities and allows the observer to see in the dark, outside the spotlight of consciousness.

Keywords: face perception, body perception, social vision, social signals, social consciousness, night vision

This chapter discusses recent findings from our own research on face and body perception with special attention to the implications of the findings for social vision. The first section is devoted to similarities between the processes underlying face and body perception. In the second section we discuss how the perception of faces and bodies is integrated. The third section tackles issues on conscious and nonconscious perception of socially meaningful signals and their neuroanatomical underpinnings. Finally, the relation between social vision and awareness is explored and notion of social consciousness is developed. Throughout this chapter we use the notions of agent vision and social vision in the sense made familiar by the expression 'night vision' to refer to various devices that expand the normal visual abilities and allows the observer to see in the dark, outside the spotlight of consciousness. Night vision is a metaphor for the enhanced abilities that allow the viewer to take advantage of nonvisible sources of information in the enviroment. For example, some animals can see well into the infrared and/or ultraviolet compared to humans, enough to help them see in conditions humans cannot.

A familiar claim in the cognitive neuroscience literature of the last decade is that many cognitive abilities have a social dimension and can usefully be grouped together under the umbrella of the social brain hypothesis. Often this notion refers to a subset of cognitive abilities that are concerned with perception of and reasoning about social objects and agents. For example, we perceive objects as we perceive people, we reason about objects as we reason about people, and, in the latter cases, the perceptual skills and reasoning abilities are labeled as social because the domain in which they are exercised is that of the social as opposed to the physical reality. In the classical hierarchical models of vision, the social dimension of object cognition is associated with the later stages of processing in temporal cortex and in prefrontal cortex.

A more radical meaning of the social dimension of perceptual and cognitive abilities is that they have a social origin. Seen in an evolutionary perspective, this amounts to the thesis that the social brain evolved in the process of and as a consequence of the demands of the social environment. The hypothesis that consciousness may have a social origin was initially put forward by Humphrey(Humphrey, 1983). He argues that our ability to be conscious of ourselves and others may have its evolutionary origin in the increasing need to collaborate with others, and the interdependence between agents created by living in extended communities.

We would like to argue that this broad social-evolutionary perspective on consciousness (p.52) may also be applied to the visual system, at least as a heuristic principle, and may orient the search for specific hypotheses about phylogenetically ancient social properties of the visual system of higher organisms. Indeed, if the latter evolved as part of this evolutionary adaptation to, and specialization for, the social environment, it makes sense to look for traces of social tuning in the brain's visual abilities, including in the early stages. In other words, a specialization for social objects may be present at different stages throughout the visual system, starting with

early vision in posterior brain regions and including later and more familiar processes in temporal cortex. This chapter discusses to what extent the evolutionary social vision framework is substantiated by a discussion on similarities between processing of faces and bodies, and by the investigation of nonconscious vision abilities reported for both classes of stimuli.

Conversely, as we propose in concluding the chapter, the evolutionary relation between consciousness and vision may also obtain in the other direction, that is, from social vision to consciousness. The co-evolution of consciousness and social-vision abilities suggests that the two may have a privileged relationship, so that social species may have a specialized ability for being aware of their co-specifics. In other words, like vision, our ability to be conscious may not be a *tabula rasa*, but may come with an evolutionary disposition to be aware of others. This social consciousness may have a strong emotional component, and it may, in part, be mediated by mechanisms on which our own body awareness is based. Our approach in this chapter is to take the issue of the functional similarities between faces and bodies as a privileged access road for clarifying social vision. The functional similarity of face and body signals challenges theories exclusively concerned with analysis of the specific visual features, and instead suggests an approach that cuts across gross physical stimulus differences, as there exist between facial and bodily expressions, to focus more on the functional and semantic properties of visual signals.

Is There a Common Social Vision Ability for Faces and Bodies?

To act effectively and adaptively, social species must rapidly perceive relevant signals about intentions and actions provided by the social environment. In the visual domain, facial expressions and body language are among the most frequent signals routinely exchanged. Because faces are parts of bodies, they often communicate the same message; their individual cues can be cumulated, increasing the changes for adaptive reactions from the observer. For example, as observers we experience similarly the negative impact of an angry face and that of an angry fist, or of an aggressive posture. The few studies that have compared explicit recognition and verbal labeling of facial expressions and bodily expressions each presented on their own, have shown, not surprisingly, that, in neurologically intact observers, both are recognized equally well.

Because facial expressions and signals provided by emotional body language are physically so different, we are interested to explore their similar functional status and significance for the observer. If there are indications that similarities in functional significance between faces and bodies already exists in the relatively early stages, then this may have some consequences for theories of social vision.

Our review of current evidence for similarities between face and body perception includes findings about overlap in the neural basis and in the temporal dynamics of face and body processes in neurologically intact observers. Furthermore, a very

valuable source of evidence in favor of the notion that faces and body perception share common neural resources comes from findings that deficits in face and body processing are possibly associated in some neurological populations. These include developmental prosopagnosics and patients with Huntington disease, as well as populations with affective-communicative disorders like autism and schizophrenia.

Functional Neuroanatomy

A mainstream approach to understanding functional neuroanatomy(certainly it was in

(p.53)

the early days of human brain imaging)is to look for distinct brain areas that more or less uniquely represent a given stimulus category. Because functional similarities are typically considered to be secondary from this perspective, they are not the focus of attention, whereas considerations about functions would possibly lead to a different cross-categorization, as recently argued(Mahon et al., 2007). Faces, objects, tools, places and, more recently, bodies have so far been prime candidates of discrete stimulus categories represented by distinct brain areas, with faces and bodies as the candidates for social vision. We first review this work before returning to the issue of functional similarities that cross category boundaries.

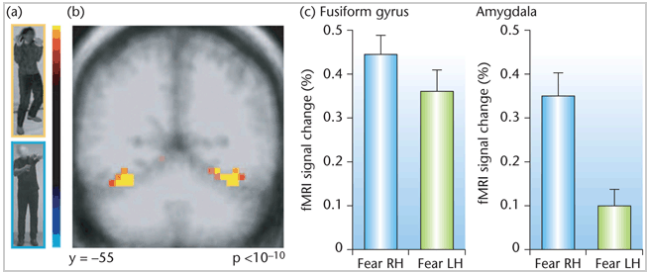


Figure 3.1 The fusiform gyrus and the amygdala show increased activation in response to bodily expressions of fear.(a)Example of the stimuli used: top, body expression of fear; bottom, emotionally neutral body posture(pouring liquid into a container). (b)Functional MRI(fMRI)activation associated with fearful compared with neutral bodies. Activation shown is in response to the fearful bodies(yellow)in the fusiform face area(FFA). No activation is seen for the neutral bodies(blue).(c)Average percentage signal change in functionally defined regions of interest in the FFA and amygdala in fearful compared with neutral body postures. From de Gelder 2006.

Many studies have reported that an area in the midfusiform cortex is selectively sensitive to faces(the fusiform face area, FFA)(Haxby et al., 1994). Another cortical area, near the middle occipital gyrus has come to the foreground because it appeared selectively activated during presentation of body stimuli and was named the extrastriate body area(EBA)(Downing, Jiang, Shuman, & Kanwisher, 2001; Grossman & Blake, 2002; Peelen & Downing, 2005; Sakreida, Schubotz, Wolfensteller, & von Cramon, 2005; Spiridon, Fischl, & Kanwisher, 2006). More recently, however, it has been shown that an area in the midfusiform cortex is also selectively activated in response to whole bodies, and this led the authors to propose a division of the

midfusiform cortex in a face vs. body sensitive set of voxels(fusiform body area, FBA) (Peelen & Downing, 2005; Schwarzlose, Baker, & Kanwisher, 2005; Spiridon et al., 2006). The latter result is consistent with our previous findings on the role of the fusiform cortex in body processing(Figure 3.1)(Hadjikhani & de Gelder, 2003).

At present, it is an open question whether novel theoretical and methodological developments will allow even more fine-grained category specificity, and even more detailed charts of cortical specialization. It is worth noting though, that most of the studies that have predominantly reported on the role for the midfusiform cortex for faces, also provided systematic evidence for face-specific activation on other cortical areas, mainly the inferior occipital gyrus(I. Gauthier, Behrmann, & Tarr, 1999; I. Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; I. I. Gauthier, 2000; Hadjikhani & de Gelder, 2003; Kanwisher & Moscovitch, 2000) and the (p.54) superior temporal sulcus(STS). Interestingly, these three areas also figure in recent reports on body representation in the brain(de Gelder, 2006a; Peelen & Downing, 2007).

It is important to note that the results about category specificity just mentioned mostly concern studies that have used neutral face and body images. Moreover, lots of these studies have contrasted faces or bodies to artifact objects, like houses or chairs, rather than to other stimuli of similar ecological and natural salience. A more challenging picture for the notion of discrete category representations emerges, however, when we turn to results obtained using facial and bodily expressions of emotion, a perspective that introduces functional considerations based on the fact that faces and bodies may convey the same affective information.

With respect to the functional neuroanatomy we found that the fusiform cortex and amygdala play an important role in processing fearful bodily expressions(de Gelder, 2006a; de Gelder, Snyder, Greve, Gerard, & Hadjikhani, 2004; Hadjikhani & de Gelder, 2003), as was previously shown for fearful facial expressions(Dolan, Morris, & de Gelder, 2001; Morris, Friston et al., 1998; Morris, Ohman, & Dolan, 1998; Rotshtein, Malach, Hadar, Graif, & Hendler, 2001a, 2001b). The original finding has now been confirmed in other studies using upper body parts(Grosbras & Paus, 2006) and whole bodies(Grèzes, Pichon, & de Gelder, 2007; Pichon, De Gelder, & Grèzes, 2007; van de Riet, Grèzes, & de Gelder, in press).

Another avenue for exploring the functional similarity between seeing faces and bodies is to measure the observers' spontaneous muscle reaction triggered by seeing facial or bodily expressions, as can be done with the tools of facial electromyography(EMG). It has been showed that observing facial expressions automatically prompts spontaneous imitation(Dimberg, 1982, 1990; Dimberg & Thunberg, 1998; Dimberg, Thunberg, & Elmehed, 2000). To investigate whether this muscle reaction is driven by automatic mimicry of the visual stimulus only, or if it implies some degree of understanding and resonance to the emotion displayed, we recorded and compared responses to presentations of different stimulus categories with

the same meaning; facial expressions, face-voice combinations, and bodily expressions communicating either fear or happiness(Magnée, de Gelder, van Engeland, & Kemner, 2007). We observed the same emotion-specific facial muscle activity(zygomaticus for happiness, corrugator for fear)for all three stimulus categories. This indicates that spontaneous facial expression is more akin to an emotional reaction than to facial mimicry and imitation of the seen face stimulus. Most notably, these emotionally congruent facial reactions occur also when the bodily expressions presented as stimuli are backwardly masked, and thus invisible to the observers(Tamietto & de Gelder, 2008b). A possible explanation for this similarity is that, for a given emotion, seeing a facial expression, a body expression, or hearing an emotional tone of voice all activate the same affect program(Frijda, 2007). The latter notion figures prominently in many evolutionary-inspired approaches to emotion. Of course this similarity in reactions across different emotion triggers begs the question of the embedding of affect programs in the brains' evolutionary history.

Clearly, none of these facts amount to claiming that any signal from the face is interchangeable with its equivalent from the body. Stimulus equivalence depends on a number of factors. It likely depends on the kind of emotion one focuses on. For example, disgust is obviously predominantly shown by facial movements and seldom involves the rest of body. Distance between agents is another factor playing an important role, as bodily expressions can communicate emotional intentions from a greater distance than facial expressions. The nature of the social relation is another dimension of intersubjective perception, and still other factors like hierarchical relation, familiarity, common goals, and friendship all determine, to some extent, the display of facial and bodily expressions(de Waal, 2005). Finally, there may be major differences in the voluntary cognitive control we have over facial and bodily expressions. In this context it is often assumed that facial expressions do come more easily under voluntary control than emotional body language does(Argyle, 1988).

Temporal Dynamics of Face and Body Processing

Do these correspondences in neurofunctional bases of face and body perception also extend to the time course of such processing? Important similarities in the temporal dynamics associated with the perception of faces and bodies have already been revealed in their electrophysiological correlates. The N170 is a well-known negative ERP-component, peaking around 170 ms at occipito-temporal sites, and is often linked to the stage of the structural encoding of faces(Bentin, Allison, Puce, Perez, & et al., 1996; Bruce & Young, 1986; Eimer, 2000b). Yet this component is also elicited by images of whole bodies(Gliga & Dehaene-Lambertz, 2005; Meeren, van Heijnsbergen, & de Gelder, 2005; Stekelenburg & de Gelder, 2004; Thierry et al., 2006). Most importantly, the electrophysiological inversion effect(Eimer, 2000a; Itier & Taylor, 2002; Watanabe, Kakigi, & Puce, 2003), consisting of a delayed and enhanced N170 deflection for inverted stimulus presentation, was elicited by both faces and bodies in contrast to control objects(Stekelenburg & de Gelder, 2004). This latter finding

suggests that the recognition of both bodies and faces relies more on global perceptual processing and structural encoding, rather than on extensive analysis of individual details of the stimuli. In keeping with these results, behavioral data(Slaughter, Stone, & Reed, 2004) have recently been obtained showing sensitivity for the canonical properties of faces and bodies alike at around 18 months. These results are supported by ERP recordings providing evidence that the configuration of faces and bodies is already processed at thrre months of age(Gliga & Dehaene-Lambertz, 2005).

Although our first EEG study(Stekelenburg & de Gelder, 2004) revealed effects of fearful expressions for face(left N170 amplitude enhanced for fear)and body stimuli(VPP amplitude enhanced for fear), in the same time window we did not obtain an effect of emotional body expression on the P1, an earlier waveform that recent studies have reported to be sensitive to emotion. A possible confounding variable may, however, have accounted for this. This previous study presented still images of fearful and neutral bodies(faces blurred)in which the fearful bodies were rather dynamic(i.e., a defensive retreating body movement), whereas the neutral instrumental actions were rather static(i.e., the action entailed only the upper body)(e.g., combing hair, drinking from a glass, holding a telephone), but the actor did not show any forward or backward whole body movement, known to induce ERP effects(Wheaton, Pipingas, Silberstein, & Puce, 2001). A follow-up study was set up to exclude the possible confounding effects of perceiving implicit body action by controlling explicitly for the instrumental action aspect(van Heijnsbergen, Meeren, Grezes, & de Gelder, 2007). Participants viewed images of whole-body actions presented either in a neutral or a fearful version. We observed an early emotion effect on the P1 peak latency around 112 ms post stimulus onset, hitherto only found for facial expressions. Moreover, consistent with the majority of facial expression studies, the N170 component elicited by perceiving bodies proved not to be sensitive for the expressed fear. In line with previous work, its vertex positive counterpart, the VPP, did show a condition-specific influence for fearful body expression. Thus, our results indicate that the information provided by fearful body expressions is already encoded in the early stages of visual processing, and suggest that similar early-processing mechanisms are involved in the perception of fear from faces and bodies.

Mageneto-encephalography(MEG)has also been used for pinning down the earliest time window of face-specific processing. First, it has been reported that the M170 is obtaned for faces, which is presumably similar to the N170 described in EEG recording(Linkenkaer-Hansen et al., 1998). More recently, an earlier component in the 100 ms time-window has been described for faces and localizes in the midoccipital region(Halgren, Raij, Marinkovic, Jousmaki, & Hari, 2000; Linkenkaer-Hansen et al., 1998). In a study using fMRI constrained MEG we investigated for the first time the very early stages of visual processing for faces and bodies conjointly(Meeren, Hadjikhani, Ahlfors, Hamalainen, & (p.56) de Gelder, 2008). We observed that, when compared to inverted faces, upright faces elicited stronger responses in a distinct area in the lingual gyrus at 55–60 ms after stimulus presentation, which was followed by a

response decrease in the calcarine sulcus and the lingual gyrus starting at around 65 ms. On the other hand, upright bodies elicited smaller responses compared to inverted bodies during the 80–90 ms latency window, in a small area in the calcarine sulcus and in a larger area involving precuneus and posterior cingulate gyrus. This category-specific sensitivity to orientation suggests that the extraction of the overall stimulus configuration of biologically salient stimuli already takes place in cortical areas V1/V2 earlier in the visual processing stream than hitherto assumed. If this would indeed be the case, such early category specificity may plead in favor of social specialization of the visual system, indicating that the early stages of this system are not a *tabula rasa* in the sense of being insensitive to the stimulus category until much later.

Findings from face and body perception and the associated speed of processing are in line with recent psychophysical and electrophysiological findings suggesting that visual categorization processes can already take place at even early latencies. In fact, Thorpe and colleagues(Kirchner & Thorpe, 2006; Thorpe, Fize, & Marlot, 1996) have found evidence for rapid visual categorization(i.e., the detection of animals versus nonanimals in natural images)to take place within the first 100–150 ms after stimulus onset.

Associated Deficits of Face and Body Processing

Valuable insight into functional association of physically different stimulus categories, like bodies and faces, are traditionally obtained from clinical populations, and this continues to be the case. For instance, do patients with face-recognition deficits also exhibit subtle body-recognition deficits and vice versa?

Prosopagnosia is a deficit in face recognition in the presence of relatively normal object recognition and may be due to brain damage in adulthood or to abnormal development of face-recognition skills. Accumulating evidence for closely related representations of faces and bodies, and overlapping brain areas sensitive to faces and bodies, raise the issue of whether developmental prosopagnosics may also be impaired in encoding bodies. We investigated the first stages of face, body, and object perception in four developmental prosopagnosics by comparing event-related brain potentials(ERPs)to canonically and upside-down presented stimuli(Righart & de Gelder, 2007) and by using fMRI. Normal configural encoding, as measured by the inversion effect was absent in three out of four developmental prosopagnosics for faces at the P1, and for both faces and bodies at the N170 component. The neural underpinnings of behavioral inversion effect explored with fMRI methods seem to underscore that the midfusiform face area is the most sensitive to face inversion and thereby the most likely candidate to subserve normal configural face processing(Yovel & Kanwisher, 2005).

Our results provide clear indications that prosopagnosics do not have this normal processing routine readily available neither for faces nor for some aspects of body perception. Yet one should not conclude, in line with the findings just quoted, that

abnormal functioning of the midfusiform gyrus is the only determinant of configural processing of faces or bodies. Notably, however, a pronounced face recognition deficit characteristic of developmental prosopagnosia may not necessarily have its origin in a deficit in the initial stages of development. It may also or even exclusively be rooted in a general anomalous processing of the configuration that is important for other stimuli besides faces, which require similar visual strategies for initial encoding and bootstraps the acquisition of visual skill that progressively build up in the course of development. Fluent processing of faces as well as of bodies mobilizes form- as well as movement-processing abilities. More importantly, they seem to require a smooth translation back and forth between form- and movement-based recognition routines and integration of the two(Figure 3.2). Thus, the notion that faces and bodies have a similar developmental course needs further study, and findings about (p.57)

associated deficits may still fundamentally be related to the fact that they present similar challenges to the visual system.

Recent studies investigating emotional body perception in individuals with autism are providing evidence that emotional body perception is impaired, partly due to the anomalous functioning of the amygdala(Grezes, Wicker, Berthoz, & de Gelder, 2009; Hadjikhani et al., 2009). Another clinical population, patients with Huntington's disease(HD), provides very valuable insights into functional similarities between facial and emotional body expressions because HD patients exhibit motor impairments as well as

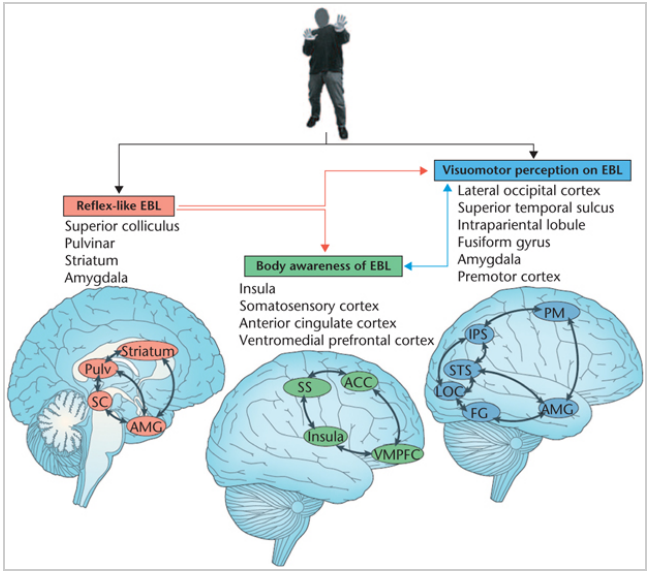


Figure 3.2 The three interrelated brain networks involved in emotional body language.(a)Reflex-like EBL(orange)involves the superior colliculus(SC), pulvinar(Pulv), striatum and amygdala(AMG). (b)Body awareness of EBL(green)involves the insula, somatosensory cortex(SS), anterior cingulate cortex(ACC)and ventromedial prefrontal cortex(VMPFC).(c)Visuomotor perception of EBL(blue)involves the lateral occipital complex(LOC), superior temporal sulcus(STS), intraparietal sulcus(IPS), fusiform gyrus(FG), amygdala(AMG)and premotor cortex(PM). Visual information from EBL enters in parallel via a subcortical(red)and a cortical(blue)input system. Feedforward connections from the subcortical to the cortical system and body awareness system are shown in red, reciprocal interactions between cortical

system and body awareness system are shown in blue. From de Gelder 2006.

cognitive and emotional deficits. So far, impairments in the ability to recognize emotional stimuli have only been investigated by using facial expressions and emotional voices. To investigate the relation between motor disorders and emotion deficits, we tested recognition of emotional body language in 19 HD patients and their matched controls with a nonverbal whole-body-expression matching task(Van den Stock, de Gelder, De Diego (p.58) Balaguer, & Bachoud-Lévi, 2005). Results indicate that HD patients are impaired in recognizing both instrumental and angry whole-body postures. Furthermore, the body-language deficits are correlated with measures of motor deficit. Taken together, the results suggest a close relationship between emotion recognition and motor abilities, and this provide an element for the explanation of the perceptual deficit previously observed for facial expressions.

The findings mentioned so far allow us to compare the neurofunctional bases and time course of faces and bodies, and to document similarities and overlaps that may testify the existence of functional commonalities between these two classes of visual signals. Note though that not all studies have tried to control for low-level visual differences, which misleadingly may acerbate category differences(Thierry, Martin, Downing, & Pegna, 2007). The way around the major differences in visual properties we opted for in our own studies has been to compare systematically scrambled, inverted, and normally presented stimuli of faces, bodies, and objects, as a means to control for low-level differences when directly comparing stimuli belonging to different categories(Meeren et al., 2008). Some caution is also required concerning the use of localizers, because often these consist of a set of faces contrasted with a set of objects where the latter consists of a variety of different objects(e.g., in the study by Yovel & Kanwisher, 2005).

Integrated Processing of Information from Faces and Bodies

Obviously, in real life faces and bodies are simultaneously present and it makes sense to assume that we react to both together and at the same time, even if we focus more on one than on the other. On the other hand, depending on a whole set of context factors and also on which specific emotion is communicated at a given moment, either the face or the body may be the privileged medium to convey that particular meaning and set the emotional tone of the interaction. There are, at present, very few empirical data that throw light on this issue. Nonetheless, it seems clear enough that context does influence how strongly the facial expression(Righart & de Gelder, 2006) and the emotional body language is appraised(Van den Stock, Righart, & de Gelder, 2007). It may well be the case that in one-to-one interactions, attention is, or appears to be, absorbed by the face. This may also be due to the fact that, by watching the face, one attends better to what is said. On the other hand, facial expressions are to some extent

under intentional control because we are more used to attend to and monitor our facial expression and because they are more under our voluntary control.

These considerations were the starting point of some recent experiments in which we investigated the impact of the unattended body expression on how observers rate the emotion in the face. In the first behavioral study, we used a continuum of facial expressions created by morphing between two anchor points consisting of a happy and a fearful facial expression, while the bodily expression remained always the same(always happy or always fearful)(Van den Stock et al., 2007). The results provided clear evidence that recognition of facial expressions is influenced by the accompanying body language. A happy face combined with a happy body is categorized as more happy, compared to when the same happy face appears on a fearful body. Likewise, a fearful face on a fearful body is categorized as more fearful, compared to when it appears in combination with a happy body expression. It should be stressed that the instructions explicitly stated to categorize the facial expression, so there was no ambiguity regarding the target for attention and classification. Moreover, the interaction and trend analysis reported in this study indicate that the influence of the body expression is a function of the ambiguity of the facial expression: the whole-body expression has the strongest influence when the face ambiguity is highest, and decreases with reduced facial ambiguity. This indicates that the merging of information across stimulus categories is driven by the perception of the meaning irrespective of the medium through which the meaning is conveyed.

(p.59) The same questions of whether and how multiple emotional expressions are integrated were addressed using a very different paradigm, which excludes potential confounds from attention and carefully controls for task demands. We used the redundant target paradigm and measured redundancy gain when two facial expressions, which could have either congruent or incongruent expressions, were presented at the same time(Tamietto, Adenzato, Geminiani, & de Gelder, 2007; Tamietto & de Gelder, 2008a; Tamietto, Geminiani, & de Gelder, 2005; Tamietto, Latini Corazzini, de Gelder, & Geminiani, 2006). Even more interestingly, we used this approach when emotional congruency was provided by the simultaneous presentation of a fearful face in one visual field and a fearful body in the opposite field, a situation in which there is no perceptual similarity between stimuli(Tamietto, Geminiani, & De Gelder, 2006). We consistently found that expressions of fear or happiness are more readily recognized when they are paired with a congruent expression, regardless of whether this is a face or a body. The fact that interhemispheric integration of emotions does not seem sensitive to the physical properties of the stimuli suggests that the emotional significance of different stimuli is extracted quite early on in the visual-processing stream and raises the possibility that body and face perception share partly overlapping neurofunctional resources.

These questions were explored in follow-up studies with methods that provide a better insight in the temporal dynamics. In a first investigation of the time course, EEG was

used(Meeren et al., 2005). The combined processing of facial and bodily expressions revealed behavioral and rapid electrophysiological effects of emotional congruency. Already at 110 ms post stimulus onset, the P1, a positive ERP component found at occipital electrode sites, significantly distinguished between matching and nonmatching angry and fearful facial and bodily expressions(Figure 3.3).

Besides emphasizing the close relationship between processing of facial and bodily expressions, these findings additionally suggest that emotional expressions in both faces and bodies are encoded within a very early stage of processing, even before the visual categorization of a stimulus as a face or a body and the recognition of the personal identity has taken place, as indexed by the time course of the N170/M170 component(Bentin et al., 1996; Eimer, 2000b; Gliga & Dehaene-Lambertz, 2005; Kloth et al., 2006; Liu, Harris, & Kanwisher, 2002; Stekelenburg & de Gelder, 2004; Thierry et al., 2006). In fact, faces or bodies that were presented in isolation as control conditions did not elicit early emotion effects on the P1-component.

Neurofunctional Basis of Face-Body Congruence Effects

In a fMRI study, we presented compound stimuli consisting of a face and a body with a fearful, happy, or neutral expression, using a task that required judging the emotion of either the face or body, as indicated by a response screen directly following the stimulus. We focused on the hemodynamic response to these stimuli in the fusiform face and body area, the amygdala, and the extrastriate body area. Significant effects, for the fusiform face and body area, and near-significant effects for the amygdala, were found with larger activity for the fearful body in contrast to the happy and/or neutral body when this expression was combined with a nonfearful facial expression, that is, happy or neutral expression. When the emotion of the body had to be judged, we observed that a fearful body elicited a larger hemodynamic response than a happy body in the right extrastriate body area regardless of which facial expression was coupled to it(van de Riet, Grezes & de Gelder, 2009).

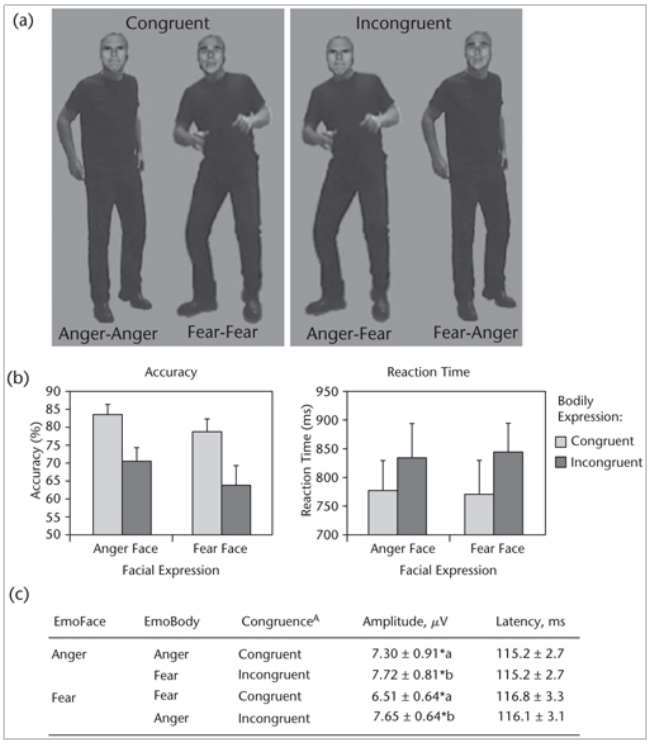
Subcortical social vision

As we remarked at the start, the notion of a brain with social-vision abilities most often reflects the notion that social skills may be attributed to some brain areas possibly reflecting the distinction between social and nonsocial categories of objects. Functionalist considerations like those already mentioned, which lump together faces and bodies carrying the same meaning, challenges a categorization based on such object properties and favors functional over physical categories. A different line of arguments in favor (p.60)

of functional analysis
comes from evolutionary
considerations, which
draw attention away from

strictly cortical taxonomies to processes in midbrain and in phylogenetically older subcortical structures. This is the area in which the notion of a brain equipped with social vision may be best implemented. In this section we review current evidence for the notion that humans have a brain with social-vision abilities and that subcortical structures are an important part of this. Comparing this to the night-vision abilities of some cameras, one might say that a brain with social vision can perceive social information "in the dark" and act under control of subcortical structures outside the realm of the light of explicit thought, deliberate reflection, and awareness.

(p.61) In human social neuroscience research, the contribution of subcortical structures has come to the foreground through recent discoveries of nonconscious affective perception, first in studies of so called subliminal perception in healthy observers, and, more recently, in studies on nonconscious perception in neurological patients.



(c)

EmoFace	EmoBody	Congruence[A]	Amplitude, μV	Latency, ms
Anger	Anger	Congruent	7.30 ± 0.91*a	115.2 ± 2.7
	Fear	Incongruent	7.72 ± 0.81*b	115.2 ± 2.7
Fear	Fear	Congruent	6.51 ± 0.64*a	116.8 ± 3.3
	Anger	Incongruent	7.65 ± 0.64*b	116.1 ± 3.1

Figure 3.3 Examples of the four different categories of face–body compound stimuli used. Congruent and incongruent stimuli consisted of the same material in different combinations. The bodies of the two congruent stimulus conditions were swapped to create a mismatch between the emotion expressed by the face and that expressed by the body. (b)Behavioural results of the facial expression task for the compound stimuli. Participants had to judge the expression of faces that were accompanied by either a congruent or incongruent bodily expression. Categorization of facial expressions in the presence of an incongruent body emotion significantly reduces accuracy and increases observers' reaction times. (c)Mean event-related potentials at occipital electrodes at scalp sites O1, Oz and O2 for the face–body compound stimuli. This so-called P1 scalp site component is sensitive for the mismatch between the facial expression and the emotional body language. Asterisks denote corresponding P values(*, $P < 0.05$; **, $P < 0.01$; and ***, $P < 0.001$), with symbols a *and b*, indicating the contrasting conditions. The A in column heading denotes main effects for amplitudes. Modified from Meeren et al., 2005.

There are now many studies in normal observers and in brain-damaged patients showing that reactions to emotional stimuli do not depend on normal visual awareness. The latter may have become impossible due to brain damage, as in the rare cases of selective striate cortex damage, or because awareness is prevented by experimental manipulation; most typically visual masking(Dimberg et al., 2000; Esteves, Dimberg, & Öhman, 1994; Jolij & Lamme, 2005; Killgore & Yurgelun-Todd, 2004; Liddell et al., 2005; Morris, Ohman et al., 1998; Murphy & Zajonc, 1993; Niedenthal, 1990; Pessoa, Japee, Sturman, & Ungerleider, 2006; Pessoa, Japee, & Ungerleider, 2005; Tamietto & de Gelder, 2008a; Whalen et al., 2004; Whalen et al., 1998b; Williams et al., 2006; Williams et al., 2004). This suggests that there might be a nonconscious perceptual subsystem for visually based affect experience and cognition. To the extent that this system is an integral part of the brain, it may also be functional, though dormant, in normal observers and not only in patients with cortical blindness(affective blindsight)(de Gelder et al. 2000). This nonconscious system seems to operate in parallel with the normal, predominantly cortical, processing routes and may have characteristics that are possibly different from that of conscious emotion recognition. The extent to which the involvement of cortical routes can be ruled out in healthy observers is still controversial, as it is still a matter of debate whether masking or other techniques, like TMS, create a situation that is a functional equivalent of blindsight or of affective blindsight(Marzi, Minelli, & Savazzi, 2004).

Nonconscious or Unattended Perception

Findings about subliminal perception in the 1950s raised the question of whether unseen information influences our conscious perception of the seen world. The most radical indications are provided by studies of patients with striate cortex lesion, which we review first. A number of studies have been devoted to similar observations in neurologically intact observers discussed next.

New experiments on affective blindsight investigated possible online interaction between the aware and the unaware modes of emotional processing, as well as the influence exerted by unseen emotions over ongoing recognition of other consciously perceived stimuli(de Gelder, Morris, & Dolan, 2005; de Gelder, Pourtois, van Raamsdonk, Vroomen, & Weiskrantz, 2001; de Gelder, Pourtois, & Weiskrantz, 2002; Tamietto, Weiskrantz, Geminiani, & de Gelder, 2007). This series of studies took advantage of indirect methods of testing which, as compared to direct “guessing” methods, cannot be influenced by deliberate response strategies used by the patient. In these methods, two stimuli are simultaneously presented, one projected to the blind field, and thus unseen by the patient, while the other stimulus is projected to the normal field and hence consciously perceived. The patient is asked to respond to the normally perceived stimulus, and conclusions about nonconscious processing are based on evidence that conscious evaluation of the former stimulus is biased by the presence of the latter unseen stimulus(Marzi, Tassinari, Aglioti, & Lutzemberger, 1986). This approach has been successful in demonstrating both visual/visual as well as cross-modal interactions(visual/auditory)between consciously and nonconsciously

perceived emotional stimuli. For instance, conscious recognition of facial expressions is speeded up if another face showing the same expression is presented in the blind field(de Gelder et al., 2005; de Gelder et al., 2001). Interestingly, the influence of nonconscious processing over conscious perception does not seem related to the physical/perceptual similarities between stimuli, but rather appears to be driven by the emotional information conveyed by the stimuli. Indeed, a bias from unseen to seen stimulus is also present when two stimuli have very different physical properties, such as a facial and a bodily expression, but represent congruent or incongruent information like, for example, a happy face paired with a fearful body expression(Tamietto, Weiskrantz et al., 2007). (p.62)

Similar findings have been reported by studies that investigate perceptual recognition of emotions in the absence of stimulus awareness in neurological populations with lesions to brain areas that are not primarily visual. For instance, a striking dissociation between the loss of conscious perception and the preservation of residual, nonconscious processing of some stimulus attributes(included emotional valence)is present also in conditions such as hemispatial neglect or visual extinction that follow from injury to the parietal lobe in the right cerebral hemisphere(Figure 3.4) (Tamietto, Geminiani, Genero, & de Gelder, 2007; Tamietto, Latini Corazzini et al., 2005; Vuilleumier, 2005; Vuilleumier & Schwartz, 2001). In these cases, however, the deficit of visual awareness is remarkably different from that shown

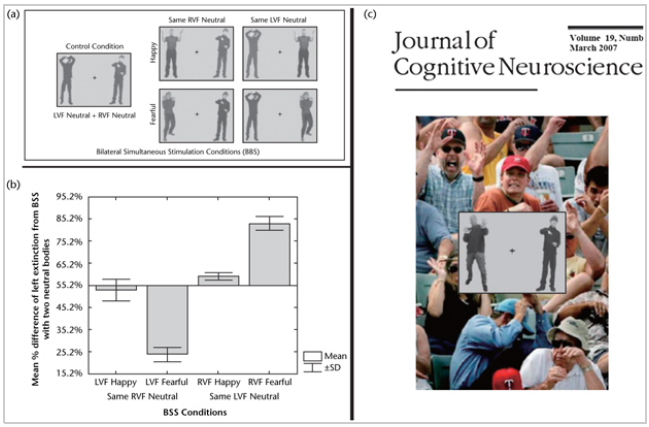


Figure 3.4 (a)Examples of the five bilateral simultaneous stimulation(BSS)displays presented to patients with hemispatial neglect and visual extinction. The five BSS conditions consisted of two neutral expressions(control condition)one left-side happy plus one right-side neutral, one left-side fearful plus one right-side neutral, one left-side neutral plus one right-side happy, and one left-side fearful plus one right-side neutral bodily expression. (b)Mean difference in the percentage of contralesional left extinction from the BSS control condition with left-side neutral plus right-side neutral bodily images.(c)cover of the *Journal of Cognitive Neuroscience* illustrating the fact that emotional bodily expression automatically summon attention and triggers similar and coordinated responses. Modified from Tamietto et al., 2007.

by blindsight patients and arises at later stages of stimulus processing that are most likely related to the ability to orient attention toward stimuli presented in a portion of the space, rather than to a defect directly due to visual perception(Driver & Mattingley, 1998).

A longstanding debate in all the areas where nonconscious perception has been reported is whether the difference with conscious vision is qualitative or only quantitative. In the latter case the difference between the conscious and the nonconscious mode is one of degree. This argument has been made in a number of studies by Pessoa and Ungerleider(Pessoa, 2005; Pessoa et al., 2006; Pessoa et al., 2005; Pessoa, McKenna, Gutierrez, & Ungerleider, 2002; Pessoa & Padmala, 2005; Pessoa, Padmala, & Morland, 2005; Pessoa & Ungerleider, 2004). Pessoa and collaborators (2005) paid attention to individual difference and discounted these in their fMRI analysis. Using a trial-by-trial (p.63) analysis they observed that masked fear expressions only triggered amygdala activation in the study participants. However, when individual differences were taken into account and data were analysed separately for the subpopulation that had seen some of the masked stimuli, the amygdala only showed a response to these "seen" trials. Pessoa and collaborators concluded that nonconscious processing of emotional expressions may be the effect of weakly conscious processing. Of course, results like these do not settle the debate in favor of consciousness as a prerequisite for processing visual stimuli, but they indicate how difficult it is for the researcher to implement conditions in which the stimulus is completely unseen.

Nonconscious Perception in Cortical Blindness

For the time being, research on affective blindsight in cortically blind persons thus presents the clearest window on nonconscious emotion perception because, when visual parameters like luminance are carefully controlled, the patients literally cannot see nor visually acknowledge the presence of a stimulus. Investigation of this condition offers a unique opportunity to understand the neurofunctional bases of emotion perception without awareness. Its importance is directly related to the fact that emotional processing in the absence of stimulus awareness is an important component of the emotional capabilities of neurologically intact individuals. Thus, studies of nonconscious vision in healthy observers can thus provide only partial support for nonconscious emotional processing and its neural underpinnings.

Until recently, investigation of nonconscious perception in blindsight had focused predominantly on basic psychophysical properties, such as discrimination of simple shapes, gratings, movement, or color(Weiskrantz, 1986, 2000). The first report that a patient with blindsight could discriminate, with a reliability exceeding chance level, the emotion of stimuli he could not consciously perceive was published by de Gelder and co-workers in 1999(de Gelder, Vroomen, Pourtois, & Weiskrantz, 1999). It involved patient GY with blindness in his right visual field following damage to his left occipital lobe, and consisted of four different experiments in which short video

fragments and still images showing different facial expressions were used as stimuli. This first exploration used a conventional method requiring the patient to guess the emotion conveyed by stimuli he remained unaware of. At that time, there was some evidence from animal and human studies that subcortical structures(like amygdale in the medial temporal lobe)were able to survey for emotionally laden stimuli in the environment and to initiate appropriate responses toward them, even before a detailed perceptual analysis in occipito-temporal cortices(LeDoux, 1996; Morris, Ohman et al., 1998; Morris, Ohman, & Dolan, 1999; Whalen et al., 1998a). The finding that blindsight subjects can discriminate something as subtle as facial expressions without the contribution of primary visual cortex is, however, less puzzling when viewed against a broader biological context. Indeed, behavioral manifestations of emotion in the face or by whatever other means, including vocalizations and body language, have a high communicative function in many species(Darwin, 1872; de Gelder, 2006b; Hatfield, Cacioppo, & Rapson, 1994).

Over the years alternative explanations that do not need to invoke a noncortical route have been put forth(Cowey, 2004; de Gelder, Vroomen, Pourtois, & Weiskrantz, 2000; Heywood & Kentridge, 2000; Pessoa, 2005). One possibility may be that simple and easily discriminated visual features(e.g., eyes wide open)are systematically associated with a specific facial expression. When this simple feature is first shown in the intact field and then in the blind one, correct responses may be based on the association of the single and easiest feature to the correct response. This possibility of interhemispheric transfer has been conclusively discarded when evidence of affective blindsight emerged in patients with total bilateral cortical blindness who are, by definition, unable to use visual information perceived in the intact field(Hamm et al., 2003; Pegna, Khateb, Lazeyras, & Seghier, 2005). (p.64)

The critical role of the superior colliculus(SC)was shown in a direct demonstration that in the absence of V1, the SC in the midbrain is essential to translate into motor outputs visual signals that cannot be consciously perceived(Figure 3.5). We showed that a stimulus in the blind field of a patient with a unilateral V1 lesion, although not consciously

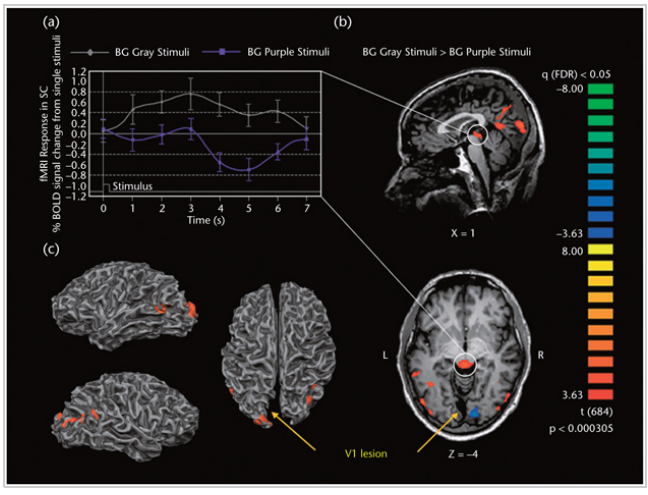


Figure 3.5 Neural correlates of the bilateral gain in blindsight patient G. Y. indicating a critical role of the superior colliculus in visuo-motor integration. Activation maps and mean percent of BOLD response in the SC for the contrast between bilateral

seen, can influence his behavioral and pupillary responses to consciously perceived stimuli in the intact field, and this is accompanied by activation in the SC. However, when the stimulus was colored purple, and was hence rendered selectively invisible to the SC that is insensitive to short wavelength light, it no longer modulated visuo-motor or pupillary responses, and the activation in the SC dropped significantly. These findings show that the SC acts as an interface between sensory and motor processing in the human brain, thereby providing an essential contribution to visually guided behavior that may remain anatomically segregated from the major geniculo-striate pathway and entirely outside conscious visual experience(Tamietto, Cauda et al., 2010). (p.65)

gain for gray versus purple stimuli. Areas colored from yellow to red are significantly more activated in the bilateral gain for gray stimuli, whereas areas from blue to green are significantly more activated in the bilateral gain for purple stimuli.(a)mean percent of BOLD signal change(±SEM)for the voxels in the activated clusters as a function of stimulus color and position.(b)Sagittal and transversal slices of G. Y.'s brain showing significant activations in the left and right SC and in extrastriate visual areas corresponding to higher responses to the condition of bilateral gain for gray stimuli.(c)Three-dimensional reconstruction of G. Y.'s brain from lateral and top view showing the occipito-temporal extrastriate areas significantly more activated by the bilateral gain for gray stimuli. The dorsal portion of the lesion to V1 is visible in top view. BG = bilateral gain; BVF = both visual fields; FDR = false discovery rate; LVF = left visual field; RVF = right visual field; SC = superior colliculus. Modified from Tamietto et al., 2010.

Is There a Subcortical Social Vision Only for Faces?

Until very recently, most investigations of human emotions predominately concentrated on perception of facial expressions(Adolphs, 2002). So, it is not surprising that affective blindsight was initially tested with facial expressions. Other facial attributes, such as personal identity or gender, were also tested with negative results, thereby suggesting that neither movement or nonemotional facial attributes are *per se* the determinant of the phenomenon. More directly, in later research, affective blindsight also emerged very clearly when still images of facial expressions were used, especially if the patients were tested with indirect methodologies that typically do not require the subjects to make guesses about visual events they do not perceive consciously(Anders et al., 2004; de Gelder et al., 2005; de Gelder et al., 2001; de Gelder et al., 2002; Pegna et al., 2005). Still unanswered is the issue of whether affective blindsight is induced by nonconscious processing of overall face configuration or by individual key features in the face. There is evidence that the eye region is particularly salient in conveying emotion information(namely of fear), and that the most ancient parts of our visual and emotion systems in the brain seem tuned

to detect this simple signal rather than the whole face configuration(Morris, deBonis, & Dolan, 2002; Whalen et al., 2004). Nonetheless, a direct test of this issue in blindsight patients is still missing.

The functional notion of social vision we put forward here suggests that other stimulus categories with very different physical visual properties and/or attributes can also give rise to affective blindsight. Under the assumption that the special role of faces is not fixed by their physical properties but by their functional ones, it can be assumed that affective blindsight is possible for physically different stimuli with similar functional properties, such as bodily expressions.

Aside from facial expressions, other stimulus categories have been used to test whether affective blindsight could be extended to stimuli other than faces. Thus far, the most studied categories are affective scenes and bodily expressions of emotions. Generally, negative results have been reported for scenes with both direct and indirect methods, suggesting that the appraisal of the emotional content of complex pictures requires cognitive and semantic processing that depend critically on conscious visual perception, which is prevented by V1 damage in blindsight patients(de Gelder et al., 2005; de Gelder et al., 2002). On the other hand, behavioral and neuroimaging results have shown that affective blindsight for bodily expressions may be at least as clearly established as that previously reported for facial expressions, and sustained by a partly overlapping neural pathway(de Gelder & Hadjikhani, 2006; Tamietto, Weiskrantz et al., 2007). This indicates that implicit processing of emotions in blindsight does not seem to be specific for faces but rather, and more generically, for biologically primitive emotional expressions that are clearly associated with action tendencies.

The use of brainimaging techniques, mainly fMRI, provided direct evidence regarding the functional areas and pathways sustaining affective blindsight and the neural structures involved in it(Anders et al., 2004; de Gelder & Hadjikhani, 2006; de Gelder et al., 2005; Morris, DeGelder, Weiskrantz, & Dolan, 2001; Pegna et al., 2005). With the use of electroencephalography and its temporal resolution of the order of milliseconds, one also gets a better idea of the temporal dimension(de Gelder et al., 2002; Rossion, de Gelder, Pourtois, Guerit, & Weiskrantz, 2000).

A source of information used less often, but eminently complementing others, is provided by measuring the peripheral physiological changes that may be induced in blindsight patients by the presentation of unseen emotions. There is initial evidence that nonconsciously perceived emotions may elicit arousal and expressive reactions in the patients that are consistent with the affective valence of the unseen stimuli, as measured by electromyography and pupillometry(Figure 3.6)(Tamietto, Castelli et al., 2009).

The neuro-anatomical underpinnings of affective blindsight are still not fully understood. Yet, in the case of nonconscious social vision, as in that of affective blindsight, theories and hypotheses are enriched by the numerous findings on affective

processing derived from animal studies, the information about pathways, and the

(p.66)

theoretical models they have produced. Earlier animal studies in rats underlined the role of midbrain structures in providing a rapid but coarse analysis of the affective value of auditory as well as visual stimuli, even without the contribution of the primary sensory cortices(Campeau & Davis, 1995; Doron & Ledoux, 1999; Jones & Burton, 1976; LeDoux, 1996; Linke, De Lima, Schwegler, & Pape, 1999; Shi & Davis, 2001). A similar subcortical pathway was also envisaged in a healthy human observer when facial expressions were subliminally presented(Morris et al., 1999). Thus, attention was suddenly focused on the functional integrity of this subcortical visual pathway in patients with affective blindsight and, indeed, the activation of subcortical structures composing this pathway has been repeatedly shown in different neuroimaging studies(de Gelder & Hadjikhani, 2006; de Gelder et al., 2005; Morris et al., 2001; Pegna et al., 2005).

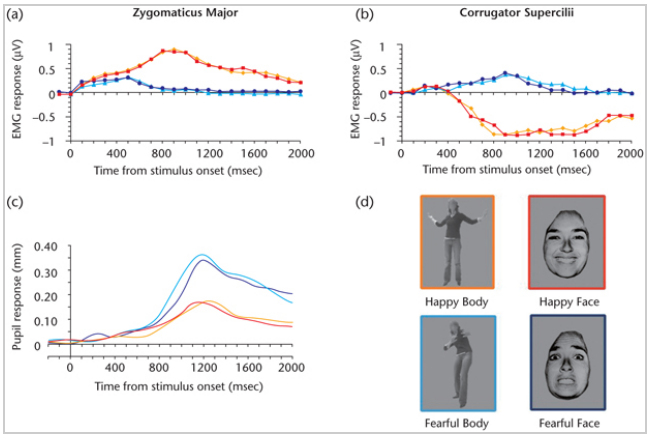


Figure 3.6 EMG and pupil responses in blindsight patient DB for unseen facial and bodily expressions of happiness and fear(a)Mean responses in the Zigomaticus Major.(b)Mean responses in the Corrugator Supercilii.(c)Mean pupil responses.(d). Examples of the stimuli used. Frame color on the stimuli corresponds to coding of EMG and pupil response waveforms to the same class of stimuli. Modified from Tamietto et al., 2009.

The involvement of the subcortical pathway in affective and, before that, nonaffective blindsight has been mostly documented in patient GY, who suffered an occipital lesion very early in life(at age 7)(de Gelder et al., 2005; Morris et al., 2001; Sahraie et al., 1997). Thus, it is possible that postlesion and experience-dependent plasticity have taken place in this patient. In this case the role of the subcortical pathway would not generalize to all patients showing affective blindsight. Even though the presentation of affective stimuli to the blind fields of other patients also activated subcortical structures like the amygdala, the functional or anatomical connectivity of the different structures putatively implicated along this route have not been directly tested in patients different from GY. Interestingly, however, subliminal emotional expressions activate in healthy subjects the same subcortical pathway that is the most likely candidate in affective blindsight following striate cortex lesions(Liddell et al., 2005; Morris et al., 1999; Williams et al., 2006). Studies that will trace the pathways involved in noncortical processing are now under way using tractography methods like

diffusion tensor imaging(DTI). (p.67)

From Social Vision to Social Consciousness

Is there a specialization of consciousness that corresponds to the brains' specialization for social vision? This is a bold question in view of the fact that our common sense notion of consciousness balks at the idea of fragmented, local, or regional subprocesses and sees consciousness as one and indivisible. Mainstream philosophical analyses are also built upon the notion that consciousness is not many but one, and almost by definition linked to constitutive singularity of the subject of consciousness(Galati, Tamietto, & Tinti, 2001). Yet, an a priori weak version of the social consciousness hypothesis is that social vision has a privileged entry into consciousness. It may be that by looking into the mechanism whereby this is made possible, we get support for the strong notion of social consciousness or at least a better understanding of what the strong notion would imply.

As a matter of fact there are multiple indications in the clinical neuroscience literature on dissociated consciousness phenomena(Marcel & Bisiach, 1988). A strong example that is relevant here concerns anosognosia. When central neurological damage yields paralysis(plegia)and/or loss of sensation, a variety of psychological phenomena related to the affected limbs may occur, whether separately or in combination, and one of them is anosognosia(Babinski, 1914). The term refers to the lack of awareness for a neurological symptom like hemiplegia following an acute brain lesion, and most often follows a right hemisphere damage. Anosognosia is also of great clinical importance because it is closely linked with successful rehabilitation, which is often ineffective as long as patients are unaware of or fail to explicitly acknowledge that their deficit exists and that they are not aware of it(Marcel, Tegner, & Nimmo-Smith, 2004). The manifestations of anosognosia are diverse. Often the patients simply ignore the plegic limb and do not recognize it as theirs. The lack of awareness may also have a variety of positive correlates going from delusions like denial of the existence or ownership of the limb to hatred of the alien object, but also, as we saw in a recent case, to admiration of scientific achievements of having been given a beautiful robotic arm.

The debate is still open whether anosognosia is a single phenomenon or a collection of loosely related ones. While the link with sensory loss, motor loss, or both is traceable, the terms *aware* and *conscious* or *unaware* are often used loosely. Marcel et al. (2004)list a deficit in afferent proprioceptive information, absence of proprioceptive phenomenal experience, or of awareness of such experience possibly due to an attentional failure; a failure to update long-term bodily knowledge(e.g., that one cannot move one's left arm); a delusory experience of limb movement.

The aspect of interest here is that the unawareness may be limited to, and specific for, the functional loss, and thereby specifically relates to the functional role of a damaged brain area(Bisiach, Vallar, & Geminiani, 1989). That is, awareness of having a

sensory/motor deficit is not inferred from immediate experience of one's performance(Marcel et al., 2004). Two recent studies have investigated what brain areas may be credited specifically(Karnath, Baier, & Nagele, 2005) or even exclusively with the loss of awareness(Berti et al., 2005). Karnath and collaborators (2005) compared lesions in a large group of hemiplegic patents following right-hemisphere lesions. They show that the right posterior insula is the most critical structure in the contrast between hemiplegic/hemiparetic patients with anosognosia vs. patients without anosognosia. The functional significance of the insula is consistent with neuroimaging results in healthy subjects, which have revealed the specific involvement of this area in the subject's feeling of being or not being involved in a movement. Thus, taken together, the normal and the anosognosic patient data underscore the role of the insular cortex for one's awareness and beliefs about the functioning of body parts. A study by Berti and collaborators (2005) adds a further dimension to this by providing information on the motor structures involved in anosognosia. They focused on the critical lesion difference associated with anosognosia. By computing the difference in focal brain damage between two groups of patients with similar left side spatial neglect and hemiplegia, one with and one without anosognosia for motor deficit, the brain damage specific to (p.68) anosognosia may be revealed. Interestingly they report that motor deficit denial was associated with lesions in areas related to the programming of motor acts, specifically Brodmann's premotor areas 6 and 44, motor area 4, and the somatosensory cortex. They conclude from this that the movement monitoring systems and the function it monitors may be implemented within the same cortical network. Provided one identifies this failure in monitoring function with what is the core phenomenon of anosognosia, we can tentatively and speculatively find support here for the notion of fragmented modular awareness. Action recognition and self-recognition may be closely related, and the role of the insula and that of motor monitoring/execution may be complementary, and both may be needed for clarifying anosognosia. For example, in a neuroimaging study in neurologically intact observers Farrer and collaborators measured brain activation as a function of whether the hand actions the subjects observed matched the movements the subjects themselves actually performed(Farrer et al., 2003). They found a modulation of activation level in two main brain areas by the degree of discrepancy between the movement executed and the movement seen on the screen. Activation in the right posterior insula decreased with a decreasing feeling of controlling the movement. When there was a mismatch between the hand actions they performed and what they saw, activity in the right posterior insula was low, whereas the activity was high when the afferent input matched the action. In contrast, in the inferior part of the parietal lobe, specifically on the right side, the less the subject felt in control of the movements of the virtual hand, the higher the level of activation was. These results suggest that action perception and awareness of execution are intimately linked, with action awareness requiring that the action is represented.

Affective Blindsight and the Mechanism Linking Social Vision and Consciousness

As we noted already, blindsight offers a unique window into the vestigial social abilities implemented in part in subcortical structures, which in neurologically intact subjects tend to be overruled by cortical processes. Nevertheless, blindsight continues to fascinate philosophers not so much because of what we may learn from it about the visual and the social visual system, but mainly because it appears as a critical test case for theories of consciousness. Affective blindsight raises issues that may be more specific than those of blindsight. One reason is that it provides a window into the brain's primitive social-vision abilities as described earlier. The other reason is that the presence of an unseen affective stimulus may give rise to a chain of affective reactions in the organism that provide the blindsight subject with nonvisual cues about the stimulus attributes. These nonvisual cues triggered by social vision may usefully complement the impoverished visual cues. For example, if emotions are characterized by the action tendencies they are associated with(Frijda, 2007), then the blindsight viewer may *sense and feel*, in a way to be described, the affective qualities of the stimulus he is presented with. This nonvisual sensation may determine his response independently of any visual awareness of it. Alternatively, for the more sceptical readers of affective blindsight findings, it may boost his weak or below- threshold input to the visually based response.

Unlike presentation of gratings or dot patterns to the blind field, presentation of affective images presumably resonates in the perceiving organism in other ways than by sending ripples through the visual system only. In future developments the scope of the debate on consciousness in perception will probably be broadened, because attention needs to be paid to the affective resonance of nonvisual stimulus processing and the ways in which this provides an indirect but efficient basis for guessing the meaning of unseen stimuli. This is already suggested by the findings about the role parietal somatosensory cortex plays in affective blindsight(Anders et al., 2004) and by similar mimicry reactions to unseen facial as well as bodily expressions(Tamietto, Castelli et al., 2009).

An evolutionary perspective on vision and emotion suggests that environmental events relevant for survival, such as affective stimuli, should be susceptible to preferential processing. Since a major constraint of sensory systems is their limited capacity to process incoming information, one means to cope with this limitation (p.69) is by emotion enhancing attention, thus leading to increased detection of salient events. Indeed, normal vision depends critically on selective attention as many stimuli often escape awareness if unattended. Numerous studies on healthy subjects using different paradigms like visual search, attentional blink, or spatial orienting tasks, have shown that people more readily pay attention to emotional than neutral stimuli, especially when they communicate possible danger(Anderson & Phelps, 2001; Compton, 2003; Dolan, 2002; Eastwood, Smilek, & Merikle, 2003; Esteves, Dimberg, & Ohman, 1994).

Studies on brain-damaged patients with neurological deficits affecting visuo-spatial

attentional selection may provide additional information and further elucidate how emotion influences attention and contributes to the making of consciousness. Following an injury to the right parietal cortex, patients frequently show a rightward attentional bias accompanied by loss of awareness for contralesional left stimuli(hemispatial neglect), especially when competing stimuli appear further to the right(visual extinction)(Driver & Mattingley, 1998). Nonetheless, the presence of emotional bodily expressions can reduce this attentional bias and help patients to temporarily regain awareness of the stimuli in the neglected(right)side of the space, as previously shown for facial expressions(Tamietto, Geminiani et al., 2007; Vuilleumier & Schwartz, 2001). This further strengthens the role played by the functional significance of the stimuli over and above their specific visual attributes, and suggests that many previous findings on emotional face processing might extend also to body processing. In this latter case, the effect of integrating facial and bodily expressions of fear across hemispheres is associated to specific peripheral psychophysiological changes, as indexed by phasic pupil-size changes. Pupillary dilation is indeed enhanced and fastened in the situation of emotional congruency between faces and bodies, whereas the effect of emotional incongruence is evident at longer latencies in the pupillary waveform.

Consistent with this perspective, preliminary data from our group indicate that emotional information is equally available from bodies and faces alike, with differences between the two possibly depending on the specific context and conditions in which they appear. For instance, facial expressions seem to be more effective in summoning attention when presented in the near(peri-personal)space of neglect patients, consistent with the prevailing role played by facial information when social interactions take place between individuals in close proximity. Conversely, however, bodily expressions have a privileged role when other people are perceived from a distance that does not allow recognition of specific facials traits, so that bodily expressions more readily recruit attention when shown in the far(extra-personal, out-of-reach)space(Geminiani, Tamietto, Rusconi, & De Gelder, in preparation).

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